THE DEEP DIVING OF THE LOON AND OLD-SQUAW AND ITS MECHANISM

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THE depths to which loons (at least the Common Loon, *Gavia immer*) and Old-squaw (*Clangula hyemalis*) can dive are impressive. On August 27, 1934, I asked Hagen Brothers, commercial fishermen on Madeline Island, Lake Superior; if they ever caught Old-squaws in their nets. They replied that "winter ducks" were taken in 12 fathoms (72 feet) of water, rarely at 15 fathoms; that the real diver was the Loon (presumably *Gavia immer*), since they had taken it at a depth of 30 fathoms (180 feet). There is no definite information on the prey that is sought by the Loon at this depth.

Recently a Common Loon was caught in a net set in Lake Mendota at a depth of about 20 feet. During a discussion of the incident, I mentioned that the Loon had been taken at a depth of 180 feet. The statement was so received as to indicate that the diving ability of the Loon and of the Old-squaw was not common knowledge.

The Common Loon, according to Forbush,[1] is reported to have been taken in fish-nets at a depth of 60 feet. Scott [2] mentions the taking of a loon off the Door Peninsula, Wisconsin, at a depth of 90 feet. Jourdain [3] cites a case of a Common Loon ("Great Northern Diver") caught in a trammel net in 30 fathoms of water. The greatest depth is recorded by Roberts:[4] a fisherman living at the mouth of the Cascade River, Minnesota, stated that he had netted loons at a depth of 200 feet in Lake Superior.

The Old-squaw is taken frequently in the Great Lakes in gill-nets set at depths of 15 to 27 fathoms (90 to 162 feet).[5] A fisherman at St. Joseph, Michigan, told Barrows [6] positively that he had taken Old-squaws repeatedly at a depth of 30 fathoms (180 feet); and Butler [7] reported that they were taken frequently at Michigan City, Indiana, at the same depth.

Ex-Governor Hoard of Wisconsin informed Forbush [1] that this duck is taken frequently in nets set at depths of 50 to 100 feet. Forbush comments: "Probably few species of diving birds reach such depths in pursuit of food." The depths reached, according to Kortright,[8] would be unbelievable were it not for the many well-substantiated records. Apparently the Old-squaw can dive as deeply as the loon. Tarrant [9] was told by Capt. Nathan Saunders that he had caught "ducks" on lines set in Green Bay, Wisconsin, at a depth of 200 feet.

The number of Old-squaws that have been netted at times is very large but not beyond belief when it is considered that some of the nets used are over 8,000 feet in length. Bacon [10] records that fishermen at Dunkirk, New York, have taken from 5,000 to 7,000 Old-squaws at one haul. Lake Erie being comparatively shallow, most of the ducks were taken at a depth of 15 fathoms, and some at 18 to 27 fathoms. According to his personal knowledge, the largest single haul at Erie was 800 ducks. A single haul on the Great Lakes in December 1934 yielded 1,500 Old-squaws.[8]

Some figures on the number of Old-squaws taken in the waters of the Door Peninsula have been published by Scott:[2] 80 were taken at a depth of 90 feet; 12 at 115 feet; and 16 at 120 feet. There is a recent illustrated note [11] on the netting of these ducks in Lake Michigan, off Saugatuck, Allegan County, Michigan. One haul has produced 400 to 500 ducks. Most of them were taken in nets set for whitefish at depths of 8 to 16 fathoms, but it is not uncommon to find them in nets set for lake trout at a depth of 30 fathoms. I received a letter from R. W. Sewers, Saugatuck, in which he states: "We take these ducks in our nets at depths ranging from 30 feet of water to 180 feet and once in a great while at depths over 200 feet. . . . Last year [March, April, and part of May, 1946] I caught 27,000 of these ducks."

The annual loss of Old-squaws through unavoidable netting is tremendous, and exceeds vastly the number killed by hunters. Dr. W. E. Saunders, who investigated this phase of the subject in 1917, found 12 tons of these ducks at one fertilizer factory. Estimating 1,500 birds to the ton, there were approximately 18,000 in the lot.[8] R. W. Sewers gives away many of the ducks for food though the edibility of this species is low. The remainder are buried. Years ago his father obtained $1.25 per dozen for them in the Chicago market. The present law prevents the sale of wild ducks, but here is a special economic problem that deserves immediate consideration.

The depths to which birds can dive is a controversial point. Dewar [12] concludes that there is no reliable record of a bird diving to a depth greater than 10 fathoms (60 feet), but admits the possibility that some species may descend to greater depths. He dismisses the records of birds caught in nets at depths greater than 10 fathoms with the suggestion that the birds became entangled in the net while it was being raised. Irving [13] considers that the diving ability of certain birds " has probably been overrated on account of their skill at concealment when emerging." Taking into consideration the number of records and the number of Old-squaws that have been taken in nets set at great depths in the Great Lakes, it is wholly improbable that they were all caught during the raising of the nets. Dr. Robert Cushman Murphy writes: "I believe that Dewar is over-conservative in doubting avian diving records of depths greater than 60 feet. There are too many known cases of Old-squaws and other diving birds being found in lobster pots, etc., at depths as great as 240 feet." [14]

Advances in knowledge of the physiology of diving birds in recent years permit us to conclude that birds can dive to great depths, and to explain the mechanism whereby this feat is accomplished. A careful study of the problem forces the conclusion that the diving bird must be capable of reducing its specific gravity to, or appoximately to, that of water. Having accomplished this change, the amount of energy required to move through the water is reduced to a minimum. Everyone who has watched grebes has observed that they can submerge the body with scarcely a ripple. Townsend remarks that the Horned Grebe (*Colymbus auritus*) "disappears suddenly with a vigorous kick, or mysteriously and quietly *sinks* in the water." [15]

The ability of a bird to contract its body is illustrated by the observations of Audubon on the Least Bittern (*Ixobrychus exilis*): "Replacing it on the table, I took two books and laid them so as to leave before it a passage of an inch and a half, through which it walked with ease. Bringing the books nearer each other, so as to reduce the passage to one inch, I tried the Bittern again, and again it made its way between them without moving either. When dead, its body measured two inches and a quarter across, from which it is apparent that this species . . . is enabled to contract its breadth in an extraordinary degree." [16]

The suggestion that water birds can change their specific gravity was advanced over a century ago. Atkinson [17] thought that the Gallinule ("moorhen"—*Gallinula chloropus*) remained submerged by grasping vegetation with its feet. A distinct contribution was made by Slaney [18] when he proposed that diving birds have the power to expel air from the body cavities prior to submergence. Reduction in specific gravity could be accomplished by expulsion of the air or by reducing the volume of the air by compression. The latter method was favored by Morris.[19] Foottit [20] thought that the specific gravity could be controlled by the extent to which the plumage was contracted by the muscles of the skin.

The observations of Coues on the Horned Grebe are pertinent: "I once noticed a singular fact connected with the power these birds have, in common with other Grebes, of sinking quietly into the water. By the respiratory process they are able to very materially reduce or enlarge their bulk, with the consequence of displacing a varying bulk of water, and of so changing their specific gravity. Once holding a wounded Grebe in my hand, I observed its whole body to swell with a labored inspiration. As the air permeated the interior, a sort of ripple or wave passed gradually along, puffing out the belly and raising the plumage as it advanced. With the expiration, the reverse change occurred from the opposite direction, and the bird visibly shrunk in dimensions, the skin fitting tightly and the feathers lying close." [21]

The extent to which the body of a bird is expanded by inhalation and contracted by exhalation is shown clearly in the paper by Zimmer [22] (See Figure 1).

The problem of diving is stated succinctly by Dr. Stresemann: "In order to force under water their specifically lighter bodies, some species must make use of the acceleration to be obtained by a steep dive or by a free fall. . . . A protracted immersion of the body through natural strength requires special construction not only in the motor, but also in the respiratory apparatus; hence the task of the extremities to shove the bird under water must be facilitated by contrivances that make possible a controlled decrease in specific gravity. The diving birds have this arrangement in their very large inspiratory air-sacs, which can be emptied at need by application of pressure on the abdomen. After exhalation the diving bird is specifically heavier than the swimming and land birds, for the decrease in pneumaticity of the skeleton runs parallel with the increase in diving ability. This pneumaticity is extremely slight in *Podiceps* [= *Colymbus*] *cristatus, Mergus, Phalacrocorax* (in contrast to those *Steganopodes* [= Pelecaniformes] that do not dive) . . . and disappears completely in *Colymbus* [= *Gavia*] and *Fratercula*. In addition, many diving birds are able to reduce their buoyancy by compression of their plumage, i.e., by pressing the enclosed air from the cloak of feathers." [23]

Frogs can regulate their specific gravity by the amount of air held in the sac-like lungs.[24] Seals frequently, if not normally, exhale prior to diving.[25] Data on the specific gravity of birds during submergence are greatly needed. It would be a comparatively simple experiment to determine the specific gravity during diving by weighing the bird and determining the volume of water displaced by submergence, preferably voluntary. Stubbs [26] found the absolute specific gravity of a freshly killed Little Grebe (*Poliocephalus ruficollis*) to be 0.86; the bulk specific gravity (the bird dry and clean with plumage unruffled and the aerial envelope kept as large as possible), 0.66; and the apparent specific gravity (the bird with feathers bound down with fine yarn in as natural a position as possible), 0.84. A Little Grebe weighing 6 ounces

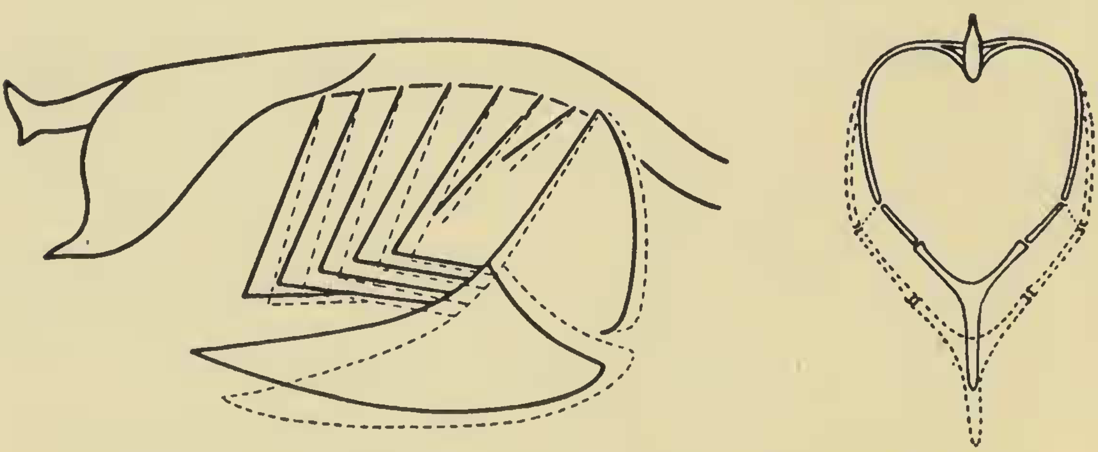

Figure 1. Lateral and frontal views of the body of a standing bird showing change of volume during expiration and inspiration. After Zimmer.[22]

and having a volume of 13 cubic inches, lost 2.24 cubic inches in the volume of its feathers under the above conditions. The method by which the specific gravity was determined is not stated. Unfortunately the above data give only a suggestion as to the actual specific gravity of the bird while submerged.

The submerged bird is apparently lighter than water. Forbush [27] mentions wounded ducks that dived and died while entangled in vegetation. They rose to the surface when set free. R. W. Sewers informed me that 95 per cent of the Old-squaws when taken from his nets will sink in water. The nets are down from 24 hours to 10 days. Some of the ducks are still warm when taken into the boat. Those that have been held under water until the plumage has become completely saturated will sink. The buoyancy of others seems to be due entirely to the small amount of air retained by the feathers. There is no evidence that water enters the interior of the duck after it has died. There is good reason for believing that the apparent specific gravity of the bird would be greater than that of water if the down feathers were completely free from air.

The absence of pneumaticity in the skeleton of the loon was mentioned (by Stresemann) above. Dr. Alexander Wetmore kindly examined the skeleton of the Old-squaw and reported that the coracoid and scapula are pneumatic, but the bones of the wing and leg are not.

Aside from the ability of the diving bird to adjust its specific gravity, there must be considered the time factor in reaching great depths and the supply of oxygen through which most of the energy is produced. Stresemann [23] states that the dive of birds seeking food seldôm lasts more than 90 seconds or exceeds a depth of 10 to 12 meters (32.8 to 39.4 feet). The longest dive for the Old-squaw that I have found recorded is 70 seconds, and the depth of the water was about 35 feet.[28] This would be a speed of only about one foot per second, but we are unaware of how much time was spent on the bottom. Dewar's rule requires 20 seconds for the first fathom and 10 seconds for each additional fathom. On this basis it would require approximately 6 minutes for a bird to reach a depth of 200 feet and return to the surface. A dive of this duration has not been recorded for the Old-squaw; however a wounded Common Loon was alive after 15 minutes of forced submersion, according to Jourdain,[3] who cites other cases of immersion lasting 8 to 10 minutes. Eaton [5] observed that the Horned Grebe could remain submerged for three minutes; and Forbush [27] thought that diving birds in general could remain under water for that length of time.

Dewar [12] gives the "average inclusive speed" of the diving bird under water as between one and two feet per second, but mentions a record of four feet per second for the Great Crested Grebe (*Colymbus cristatus*). Some of the diving birds show remarkable speed under water for brief periods. Coues [21] states that the Pacific Loon (*Gavia arctica pacifica*) shot through the water with "marvellous swiftness." Regarding Holboell's Grebe (*Colymbus grisegena holböllii*), Cahn wrote: "The speed which is developed under water is marvelous, at times it being almost impossible to follow its movements, which were so rapid that the bird appeared more like a large, gray fish darting about." [29] In one case the grebe remained under water for over a minute and reappeared more than 200 feet distant. It is evident that a bird with sufficient incentive can travel under water at far greater speeds than have been assumed.

The grebes and mergansers, according to Brewster,[30] do not compare with the loon for swiftness and distance traveled under water. He shot a loon with a .44 caliber rifle and gives the following remarkable example of vitality: ". . . the heavy bullet passed directly through the middle of her neck, about three inches above the body, partially shattering some of the vertebrae and cutting the jugular vein, yet she dove twice after receiving this ghastly wound, going each time a long distance under water. When I finally came up with her, she was swimming on the surface with head and neck erect and so vigorously that I had to make use of my shot gun before I could lay hands on her." Jourdain [3] mentions that a wounded Common Loon, attached by a line to a 13-foot boat, was able, while submerged, to tow the craft.

Disbelief in the capability of birds to dive to great depths has been based on false assumptions as to the source of the oxygen required. Forbush [27] believed that preparatory to a dive the bird filled its lungs with air; and that "extreme propulsive efforts" were required to force the buoyant body through the water. Dewar [12] states that the maximum vital capacity is "controlled initially by the amount of respirable air the bird can breathe into its lungs and air-sacs." This is not the case.

Oxygen needs of the diving bird are met in a way differing decidedly from that of the non-diver. Krogh says: "The main difference between a diver and a non-diver appears to be in the regulation of the circulation which allows the diver to reduce greatly the blood-flow to the muscles and perhaps also to the other organs and to reserve the supply mainly for the central nervous system." [31] The diver is also much more resistant to carbon dioxide than the terrestrial animal and can withstand breathing 5 to 6 per cent oxygen for a long time. During submergence the diving bird places little dependence on free oxygen. The main source of oxygen is the oxyhemoglobin and oxymyoglobin stored in the muscles. The dark color of the flesh of waterfowl is due to these substances. This oxygen is loosely combined chemically and becomes readily available when needed. Not only has the diving bird a high tolerance for carbon dioxide, but, as the tension of this gas increases, more oxygen is liberated from the oxyhemoglobin.

Further energy is derived from the formation of lactic acid from the glycogen in the tissues without the intervention of oxygen. The oxygen debt created cannot be paid until the bird rises to the surface and resumes normal respiration.

The ability of aquatic birds to prolong life under involuntary submergence is extraordinary. When the domestic duck was held under water, Bert [32] found that it would resist asphyxiation for a maximum of 16 minutes. Richet [33] closed the trachea with a ligature and extended the survival to 27 minutes. The longer survival in this case was attributed to the air forcibly retained in the lungs and air-sacs. The domestic duck is a "puddler"; different data are to be expected for a diving duck. Land animals when submerged expend their energy in violent effort. The contrary is true in general of aquatic animals. Bert observed that the domestic duck when forced under water usually remained still and endured asphyxiation quietly. A hen struggled and survived but 3.5 minutes. The Old-squaws netted in the Great Lakes die without struggling. The nets are torn only by the weight of the birds when the nets are lifted or during the removal of the entangled birds.

Paton [34] and Huxley [35] made the interesting discovery that posture produces apnœa, i.e. partial suspension of breathing. When a duck dives with neck extended, apnœa follows automatically. Apnœa also results from posture without contact with water. However, in air, regardless of the position of the body, if the duck can turn its head so that the dorsal surface is upward, breathing can be resumed. Ostensibly the essential difference between flight and diving posture is that one is horizontal and the other vertical. However, contact with water may also play a part in producing apnœa since the Common Loon will travel submerged a long distance in shallow water, where it must take a horizontal posture.

There are apparently no physical or physiological reasons why some exceptionally skillful individuals among diving birds cannot descend to a depth of 200 feet. There is ample evidence that this depth is actually reached.

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